

Latent power of basking sharks revealed by exceptional breaching events

Journal:	<i>Biology Letters</i>
Manuscript ID	RSBL-2018-0537.R1
Article Type:	Research
Date Submitted by the Author:	17-Aug-2018
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Subject:	Behaviour < BIOLOGY, Biomechanics < BIOLOGY
Categories:	Biomechanics
Keywords:	shark, energetics, performance, power, bio-logging

1 **Title: Latent power of basking sharks revealed by exceptional breaching events**

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16 **Abstract:** The fast swimming and associated breaching behaviour of endothermic mackerel
17 sharks is well suited to the capture of agile prey. In contrast, the observed but rarely
18 documented breaching capability of basking sharks is incongruous to their famously languid
19 lifestyle as filter-feeding planktivores. Indeed, by analysing video footage and an animal-
20 instrumented data logger, we found that basking sharks exhibit the same vertical velocity (~5
21 m/s) during breach events as the famously powerful predatory great white shark. We estimate
22 that an 8-m, 2700-kg basking shark, recorded breaching at 5 m/s and accelerating at 0.4 m/s²,
23 expended mechanical energy at a rate of 5.5 W/kg; a mass-specific energetic cost comparable
24 to that of the great white shark. The energy cost of such a breach is equivalent to around
25 1/17th of the daily standard metabolic cost for a basking shark, while the ratio is about half
26 this for a great white shark. While breaches by basking sharks must serve a different function

27 to white shark breaches, their similar breaching speeds questions our perception of the
28 physiology of large filter-feeding fish.

29 **Introduction, Results & Discussion:** Mackerel sharks (Order Lamniformes; Family
30 Lamnidae) including the white and mako shark are famous for their high-speed predatory
31 tactics. This strategy of attack is facilitated by adaptations including a streamlined body
32 shape, caudal fin with a high aspect ratio (Fig. 1A) and, in several species, regional
33 endothermy[1]. Because prey are typically on or near the water surface and are ambushed
34 from below, predation by these sharks often results in breaching, e.g.[2-4]; an iconic
35 behaviour in this group. By contrast, the closely related but ectothermic basking shark (Order
36 Lamniformes; Family Cetorhinidae) filter-feeds on zooplankton in cool temperate waters (8-
37 16°C)[5]. Given the immobility of planktonic prey and the languid foraging behaviour of
38 basking sharks, it may be expected that the performance capacity between basking sharks and
39 other lamniformes is quite different. However, anecdotal observation of breaching in basking
40 sharks[6, 7] suggests that they exhibit high swimming speeds and hence high power outputs
41 (Fig. 1B).

42 To investigate this phenomenon, we compared the swimming performance of basking sharks
43 when breaching to that of predatory white sharks exhibiting the same feat. We analysed video
44 sequences for both species (see Methods; Supplementary 1) to estimate vertical swimming
45 speeds at the moment of breach based on the duration that their approximate centre of mass
46 (CoM) was out of the water[8]. Both basking sharks and white sharks breach at similar angles
47 (typically around 75° from horizontal) and similar speeds (basking sharks: 5 m/s, SD 0.6,
48 N=20; great white sharks: 4.8 m/s, SD 0.8, N=18; Fig. 1C).

49 To provide new visual and biomechanical insight into the moments leading up to breaching in
50 basking sharks, we report on the first basking shark breach captured via an animal-borne data

51 logger (see Methods and Supplementary Fig. 2). These data show the change in locomotory
52 mode from slow and steady horizontal swimming by a basking shark to a rapid near-vertical
53 ascent and subsequent breach (Fig. 2; Supplementary Fig. 3; Supplementary video). This
54 deployment (at the same location as the aforementioned basking shark video recordings; see
55 methods) yielded video footage, tri-axial acceleration data and depth data which revealed the
56 animal (an 8-m male) suddenly switching from slow tail-beat (~ 0.2 Hz), steady 'cruise'
57 swimming near the sea floor to a rapid, continuous acceleration up through the water column
58 culminating in a near-vertical breach (Fig. 2). In just over 9 s and ten tail beats, the shark
59 accelerated from a depth of 28 m to the surface, breaking the water's surface at a steep angle.
60 The shark's CoM cleared the water for 1.0 s and peaked at a height of 1.2 m above the
61 surface (Fig. 2). To achieve this breach, the shark exhibited a 6-fold increase in tail beat
62 frequency above that applied during cruising (to 1.2 Hz) (Fig. 2), and attained a vertical speed
63 of 4.9 m/s (and an absolute speed of ~ 5.1 m/s; Supplementary Fig. 4), which is consistent
64 with the mean breach speeds estimated from the onshore video of other basking sharks. This
65 estimate of vertical velocity at the surface based on the duration that the CoM was out of the
66 water (Fig. 2d red line) concurs with the rate of ascent during the final second of submersion
67 recorded by the CATSCAM on-board depth sensor (Fig 2d, blue line), supporting the validity
68 of the first principles approach to estimating vertical velocity at the point of breaching[8].

69 We compared power output during breaching events in the two species. Mass-specific power
70 required to accelerate a shark is $(av + kv^3l^{-1})/\eta_h$, where l is the length of the shark, v and a are
71 its swimming speed and longitudinal acceleration, η_h is the hydrodynamic propulsion
72 efficiency, and k is a shark-specific coefficient depending on the body shape, fins area to
73 body area ratio, and on the associated Reynolds number [9] (Supplementary 4). Being
74 morphologically similar (Fig. 1a), we propose basking and white sharks have comparable

75 values of k (0.112 and 0.087, respectively; Supplementary 4) and the same η_h (0.7, *ibid.*).
 76 Consequently, an 8-m (7.4 m fork length) basking shark swimming at a constant 5 m/s will
 77 use 2/3 the mass-specific power of a 4-m (3.7 m fork length) white shark at the same speed.
 78 We estimate that an 8-m, 2700-kg basking shark swimming at a constant 5 m/s will need to
 79 generate ~ 2.7 W/kg mass of mechanical power; accelerating at 0.4 m/s^2 at that same speed
 80 would double the power requirement (Supplementary 4). Given that the maximal power of
 81 locomotive muscles is at least 50 W/kg muscle [10], these estimates imply that the breaching
 82 speed of the basking shark was not limited by its maximal power.

83 We estimate the mechanical work needed for breaching as $(k_E/\eta_h)E_k$, where $E_k = mv^2/2$ is
 84 the kinetic energy of the shark when leaving the water, and k_E is a certain coefficient
 85 (probably bounded between 1.3 and 1.5) depending on the acceleration profile and body
 86 dimensions (Supplementary 4). An 8-m basking shark must have used 63-72 kJ of
 87 mechanical energy to breach at 5 m/s. To supply this energy, its muscles used 2.6-3 moles
 88 ATP, mostly furnished by anaerobic catabolism [11, 12] of muscle-stored glycogen [13, 14].
 89 6-7 moles of ATP are required to restore that glycogen post-breach [11, 12]. Thus the full
 90 energy cost of breaching is approximately 9-10 moles ATP.

91 We estimate the standard metabolic rate (SMR) of a shark as $P_0 = k_p m^\alpha e^{-k_\tau/\tau}$, where τ is the
 92 absolute body temperature, and k_p , α and k_τ are certain phenomenological parameters. Using
 93 typical values of these parameters, an 8-m basking shark at 15°C has an SMR of about 2
 94 mmol ATP/s (6.8 mol/h). Thus a single breach is energetically equivalent to 1.3-1.5 SMR-
 95 hours (5 to 6% of its minimal daily requirement), of which 0.9-1 SMR-hours is the 'debt' to
 96 pay post-breach. The ratio $R = (k_E/\eta_h)(E_k/P_0)$ can be interpreted as the relative cost of a
 97 breach, and it is indicative of (but not equal to) the time the breaching animal will take to

recover. This ratio is proportional to $m^{1-\alpha} e^{k_{\tau}/\tau}$, suggesting that a larger animal (large m) with a lower body temperature (small τ) will need longer time to recover (see also [15]). In fact, the R -ratio of a 2700-kg basking shark at 15°C is twice that of a 900 kg great white shark at 23°C. This slow recovery of a large, ectothermic animal undertaking high-powered burst activity may explain why basking sharks do not breach at even higher speeds. White sharks typically breach only once but have been observed exhibiting full breaches up to three times in succession; as far as we are aware there are no data on whether basking sharks ever breach successively[4].

As to the function of breaching events by basking sharks (expensive as they are), there are many possible explanations. Such behaviour by white sharks in the absence of prey is common and considered to act as social communication[16]. Basking shark breaching may serve a similar function, or multiple functions including dominance, mating displays, parasite removal, prey aggregation and/or evasion of predators. Whatever the purpose of this behaviour, the similar breaching speeds of basking sharks and predatory lamnids questions our perception of the physiology of large filter-feeding fish and demonstrates that similar body designs can be well suited to very different lifestyles.

Methods

Data collection

Basking shark videos were recorded in 2015 at Malin Head, Ireland (60 fps⁻¹). 27 high density (HD) videos were captured of 600 breach events over 90 h. White shark videos were recorded in 2009 at two sites in South Africa, during predation attempts on Cape fur seals (*Arctocephalus pusillus pusillus*) using seal shaped decoys. 22 HD videos were recorded. Vertical breach speeds presented in Supplementary Table 1 and Fig. 1.

In 2013, a Customized Animal Tracking Solutions integrated multichannel data logger (CATSCAM) was deployed onto an estimated 8-m male basking shark at Malin Head, Ireland (55.37N, 007.40W) (Supplementary Fig. 2). Three hours of concurrent video footage and accelerometer data were retrieved from the deployment. A single breaching event was identified during the initial visual inspection of the video files (Supplementary video; Supplementary Fig. 3), and cross-referenced with the corresponding accelerometry and depth data (Fig. 2). The CATSCAM was dislodged from the shark's dorsal fin during the breach event at the moment of re-entry to the water, ending the deployment.

Data analysis

The time that the approximate centre of mass of each shark was out of the water during a breach, t_a , along with its body angle on exit from the water, were estimated from video footage. The observed angle of the shark's body at the moment of breach was unclear when the breach was angled towards or away from the camera position, thus, only 20 of the 27 basking shark breach videos and 18 of the 22 white shark videos allowed the body angle at the moment of exit to be estimated. The average angle was approximately 75°. Maximum vertical height of the centre of mass, h , along with vertical breach velocity v_v , were estimated using first principles with $v_v = gt_a/2$ (g is gravitational acceleration) and $h = v_v^2/2g$.

When analysing CATSCAM data, t_a was estimated using on-board video. v_v was estimated from t_a as before, but also by differentiating depth (as recorded by the logger) with respect to time. Absolute velocity of the shark at breach was estimated from v_v using the average breaching angle observed from the shore-based recordings (75°).

Drag, power and mechanical work needed for a breach were estimated after [9] (Supplementary 4). Mechanical work was converted into moles ATP using the factor of 24

144 J/mmol ATP¹⁹. The basic metabolic rate was approximated with $P_0 = k_p m^\alpha e^{-k_\tau/\tau}$, where m is
 145 the body mass, τ is the absolute body temperature, whereas k_p , α and k_τ are certain
 146 phenomenological parameters. Following[9], we have used $k_p=127 \text{ mol ATP/s} \cdot \text{kg}^\alpha$, $\alpha = 0.8$,
 147 and $k_\tau = 5020 \text{ }^\circ\text{K}$ after Ref. 15. The mass of a basking shark was estimated with al^b , where l
 148 is the fork length, whereas a and b are phenomenological constants. We have used $a = 6.54$
 149 kg/m^3 and $b = 3$ (Supplementary 4). The fork length of a basking shark was estimated at 93%
 150 of its total length – as for the great white. This produces a value of 2693 kg, which is very
 151 similar to the estimate of 2670 kg based on a power law best fit line of known data for
 152 basking shark lengths and masses reported in a review[17].

153

154 **Ethics**

155 Consent was obtained from The National Parks and Wildlife Service, Department of Arts,
 156 Heritage and Gaeltacht, Ireland.

157

158 **Data accessibility**

159 All data are included in the manuscript or in the supplementary material.

160 **Author contributions**

161 EJ and JH conceived and designed the study. EJ collected the animal borne logger data and
 162 secured research funding for field work in Ireland. AK and BW collected all other video data.
 163 GI, LH and NP led the analysis with additional input from EJ. All authors discussed the
 164 results and provided extensive comments on the manuscript in terms of analysis,
 165 interpretation and writing. All authors approved the final version and have agreed
 166 accountability for all aspects of the work.

Competing interests

We have no competing interests.

Funding

Funding was provided by the Inishowen Development Partnership.

Acknowledgements Thank you Nikolai Liebsch and Peter Kraft of Customized Animal Tracking Solution, the volunteers of the Irish and Inishowen Basking Shark Study Groups and Morne Hardenberg and Mark van Collier of Atlantic Edge Films.

Figure captions

Figure 1: Comparing basking (left panel) and white (right panel) sharks. a) The external morphology of these species is similar; b) breaches by these species; c) vertical breach velocity as determined from video analysis; means and one standard deviation. Illustrations reproduced with permission of Marc Dando, and breaching images credited to Bren Whelan and White Shark AfricaTM.

Figure 2: CATSCAM data logger data showing the a) depth, b) lateral acceleration, c) tail beat frequency (TBF) and d) vertical speed of an 8-m male basking shark immediately prior to breaching. The red line in (d) indicates the independent estimate of vertical breach speed based on first principles and time the dorsal fin-mounted video camera was out of the water during the breach. Selected still images at various stages of the video recording (see Supplementary video) are indicated by black arrows.

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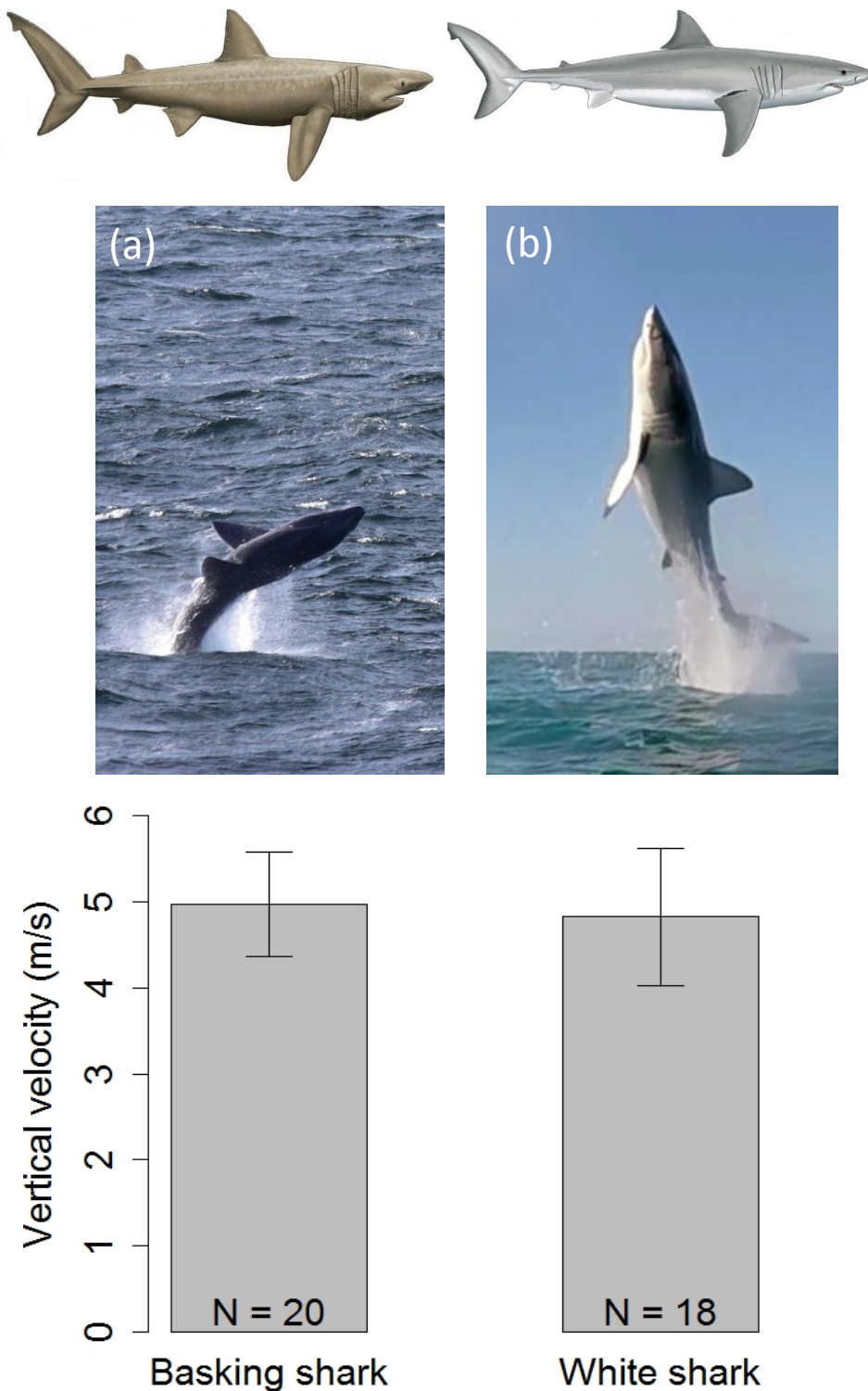


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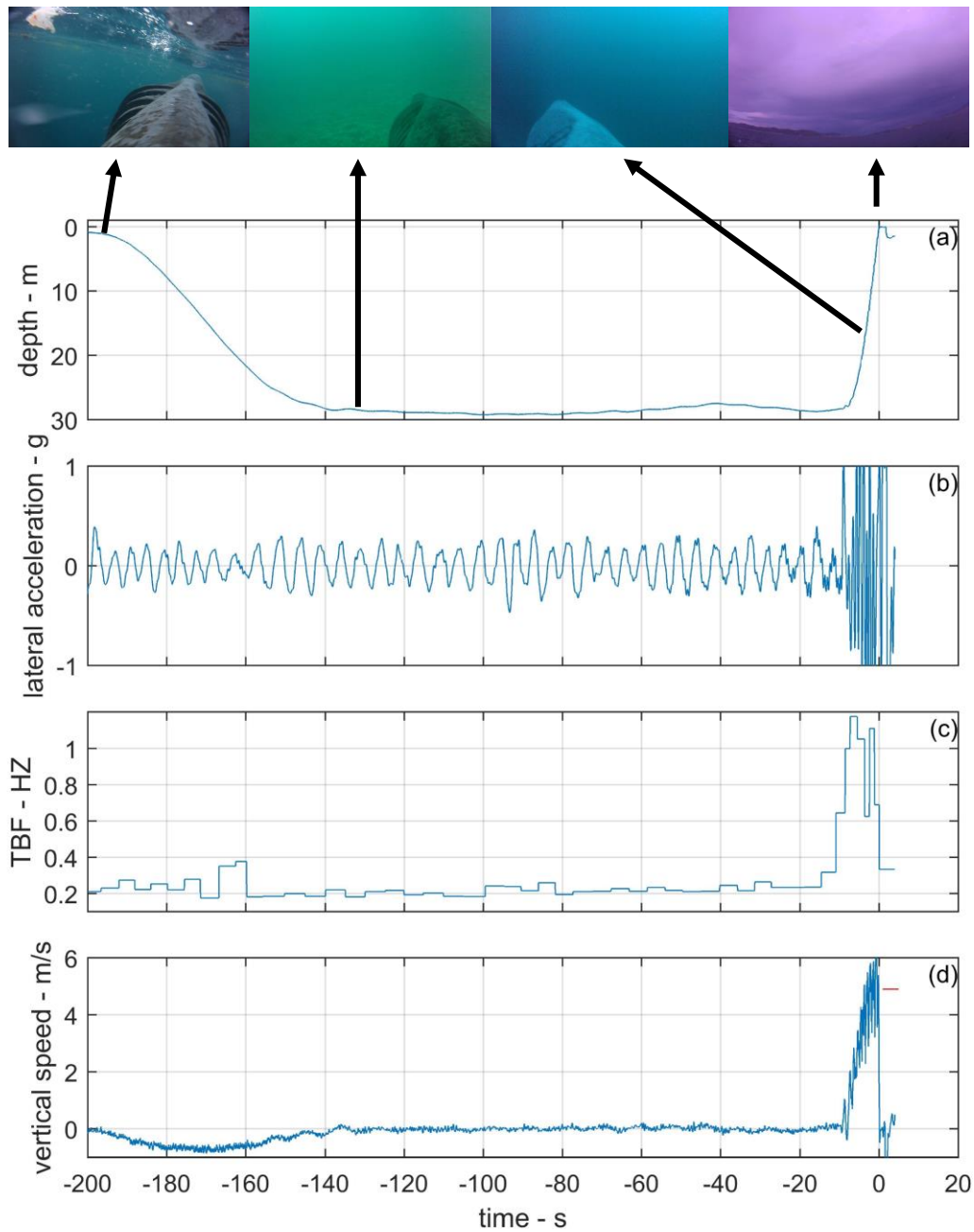


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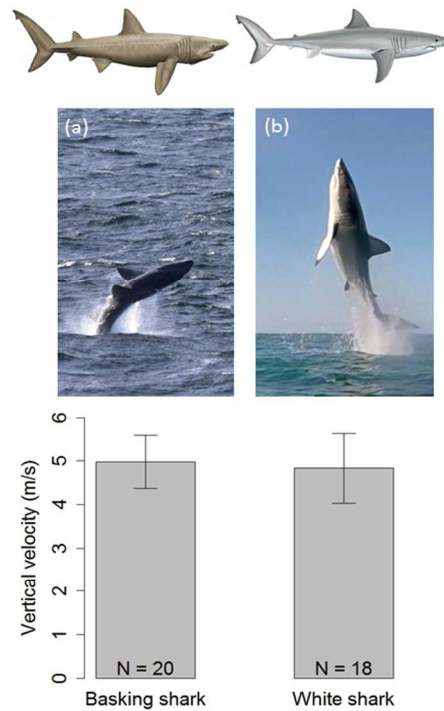


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FIG 1

190x338mm (96 x 96 DPI)

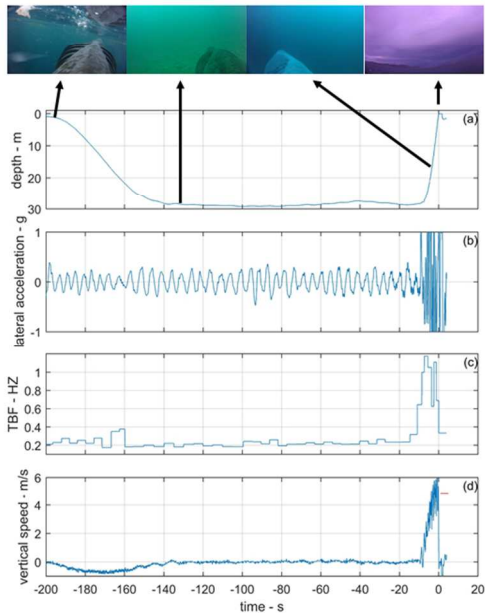


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FIG. 2

190x338mm (96 x 96 DPI)